# **REVIEW ARTICLE**

# Will Culling White-Tailed Deer Prevent Lyme Disease?

# K. J. Kugeler<sup>1</sup>, R. A. Jordan<sup>2</sup>, T. L. Schulze<sup>3</sup>, K. S. Griffith<sup>1</sup> and P. S. Mead<sup>1</sup>

<sup>1</sup> National Center for Emerging and Zoonotic Infectious Diseases, Division of Vector-Borne Diseases, Centers for Disease Control and Prevention, Fort Collins, CO, USA

<sup>2</sup> Tick-borne Diseases Program, Monmouth County Mosquito Control Division, Tinton Falls, NJ, USA

<sup>3</sup> 9 Evergreen Court, Perrineville, NJ, USA

# Impacts

- Deer population reduction is often cited as a possible Lyme disease prevention measure, but the effectiveness of this method in reducing human disease risk is not well understood.
- Complete elimination of deer from isolated settings, such as islands, can have a substantial effect on tick reproduction, but deer reduction short of elimination has yielded mixed results, and evidence of an effect on human disease risk is limited.
- At present, the evidence is weak regarding deer control as a standalone intervention to reduce human Lyme disease risk.

# Keywords:

Lyme disease; deer; deer reduction; tick; public health intervention; prevention

## Correspondence:

K. J. Kugeler. Centers for Disease Control and Prevention, National Center for Emerging and Zoonotic Infectious Diseases, Division of Vector-Borne Diseases, 3156 Rampart Road, Fort Collins, CO 80521, USA. Tel.: 970 221 6400; Fax: 970 494 6631; E-mail: kkugeler@cdc.gov

Received for publication July 15, 2015

doi: 10.1111/zph.12245

Although it seems obvious that killing animals should reduce the amount of damage they cause, the relationship is rarely straightforward. –Michael Conover in 'Resolving Human-Wildlife Conflicts'

# Introduction

Lyme disease is a zoonotic infection caused by certain genospecies of *Borrelia burgdorferi* sensu lato and transmitted in the eastern United States by *Ixodes scapularis*, the blacklegged tick. The approximately 2-year life cycle of *I. scapularis* is characterized by three blood-feeding life stages (larva, nymph and adult), with most human infections due to nymphal-stage *I. scapularis* (Piesman and Spielman,

Summary

White-tailed deer play an important role in the ecology of Lyme disease. In the United States, where the incidence and geographic range of Lyme disease continue to increase, reduction of white-tailed deer populations has been proposed as a means of preventing human illness. The effectiveness of this politically sensitive prevention method is poorly understood. We summarize and evaluate available evidence regarding the effect of deer reduction on vector tick abundance and human disease incidence. Elimination of deer from islands and other isolated settings can have a substantial impact on the reproduction of blacklegged ticks, while reduction short of complete elimination has yielded mixed results. To date, most studies have been conducted in ecologic situations that are not representative to the vast majority of areas with high human Lyme disease risk. Robust evidence linking deer control to reduced human Lyme disease risk is lacking. Currently, there is insufficient evidence to recommend deer population reduction as a Lyme disease prevention measure, except in specific ecologic circumstances.

1979; Piesman et al., 1986; Mather et al., 1990). As the incidence and geographic distribution of Lyme disease in the United States continue to expand, identification of effective and acceptable disease prevention options should be a public health priority.

In theory, Lyme disease prevention can occur at multiple levels: individual-level personal protective measures (e.g. repellent use or daily tick checks); household-level measures (e.g. landscape modification or acaricide treatment); and community-level interventions (e.g. deer control or acaricide treatment of deer) (Mead, 2011). Effective community-level interventions hold promise because of their potential to provide a broader spatial effect without reliance on individual human behaviour to achieve success.

White-tailed deer (Odocoileus virginianus) are an important source of blood for adult blacklegged ticks but are not themselves susceptible to *B. burgdorferi* infection and are not reservoirs for infection (Piesman et al., 1979; Anderson and Magnarelli, 1980; Main et al., 1981; Telford et al., 1988; Wilson et al., 1990a). Several studies have suggested some level of correlation between deer abundance and blacklegged tick abundance (Piesman et al., 1979; Anderson and Magnarelli, 1980; Schulze et al., 1984, 2001; Wilson et al., 1985, 1990b; Daniels et al., 1993; Stafford, 1993; Duffy et al., 1994; Daniels and Fish, 1995; Ginsberg and Zhioua, 1999; Rand et al., 2003; Ginsberg et al., 2004; Jordan and Schulze, 2005; Werden et al., 2014). The marked increase in deer abundance over the last several decades has been implicated by some researchers in the emergence of tickborne diseases in the north-eastern United States (Telford, 2002; Stafford, 2007) despite similar overabundance of white-tailed deer in areas where Lyme disease is extremely rare, and multiple other factors that contribute to the enzootic cycle (Ostfeld, 2011; Kilpatrick and Randolph, 2012; Levi et al., 2012).

In both the scientific literature and lay publications, local reduction of deer populations has been proposed as a community-level intervention to reduce Lyme disease incidence (Stafford, 2007). This review provides a critical assessment of the available scientific evidence regarding deer population control. We first summarize the evidence regarding the effect of deer control on tick populations, followed by the evidence regarding the effect on human Lyme disease risk. Lastly, we evaluate the validity and generalizability of available data, and discuss the feasibility of deer control as a prevention measure.

## Methods

Search terms used on PubMed were 'deer and Lyme disease' and 'deer and ticks'; manuscripts that specifically referred to experimental deer reduction or elimination and either blacklegged tick abundance or human Lyme disease as an outcome measure were included. Citations within those articles were searched in order to identify additional applicable references, including book chapters. Only studies conducted in the United States were considered and no exclusion criteria for study quality were set. Available unpublished data were included where indicated.

# Results

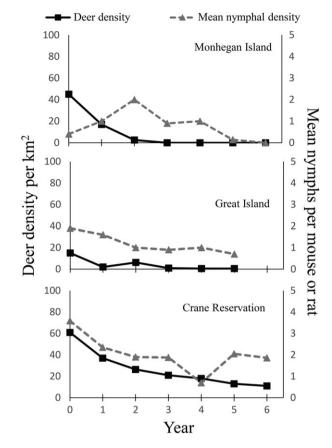
# Effect of deer control on blacklegged tick abundance

The effect of localized deer elimination on tick abundance has been assessed in only one study, conducted on Monhegan Island, a small island 16 km off the coast of Maine. The deer herd (approximately 100 animals) was eliminated between November 1996 and March 1999 (Table 1) (Rand et al., 2004). The initial deer density was back-calculated as 45 deer per km<sup>2</sup> based on number of deer removed. Hostseeking adult tick abundance was measured by flagging vegetation near trails each October (mean annual flagging hours = 19.6), while nymphal and larval abundance was evaluated on trapped Norway rats, the principal reservoir for B. burgdorferi on the island. The measured abundance of questing adult ticks increased nearly 4-fold from the year after deer reduction began to the year the last deer was removed. Prevalence of B. burgdorferi in adult ticks initially rose from 45% to 75%, before declining along with numbers of host-seeking adult ticks. Three years after deer elimination, adult ticks were rare and nymphs and larvae were absent (Fig. 1). Subadult I. scapularis have not been detected on Monhegan Island since 2002, although questing adults remain rare but present, likely through reintroduction by birds (Elias et al., 2011).

Several studies have examined the effects of deer reduction short of elimination on blacklegged tick abundance. On Great Island, a small peninsula adjacent to Cape Cod, Massachusetts, the deer population was reduced from 15 deer per km<sup>2</sup>, estimated by direct observation surveys, to <2.3 deer per km<sup>2</sup> during 1982–1983 (Wilson et al., 1984, 1988). Nymphal tick abundance declined somewhat gradually from roughly 1.9 to 0.7 per trapped mouse by 3 years following deer removal (P < 0.01) (Table 1) (Fig. 1). Adult tick abundance was not measured, although questing adults were anecdotally noted to be more abundant following deer removal. In the years following the intervention, rare deer roamed the small peninsula and blacklegged tick abundance remained at roughly 'a tenth of the preintervention magnitude' (Telford, 2002), although no specific data in support of this estimate have been published.

At the Richard T. Crane Jr. Memorial Reservation in coastal Ipswich, Massachusetts, most of which is a 9-kmlong barrier island, the deer population was reduced from approximately 62 to 11 deer per  $\text{km}^2$  over 7 years (Table 1) (Deblinger et al., 1993). Deer density was determined by a combination of direct observation surveys and estimated demographic parameters (e.g. births, harvest and non-harvest deaths). Tick abundance on trapped mice initially declined but then increased despite decreasing deer abundance (Fig. 1). After accounting for changes in mouse density, larval tick burden was significantly reduced (P < 0.001), while nymphal burden was not (Fig. 1). Post hoc, the authors also evaluated the association when restricting data only to months when each tick life stage is most active and reported statistically significant reductions in both larvae and nymphs. Over the course of the study, as deer density declined 4- to 5-fold, the adult female tick infestation on harvested female deer increased to the same

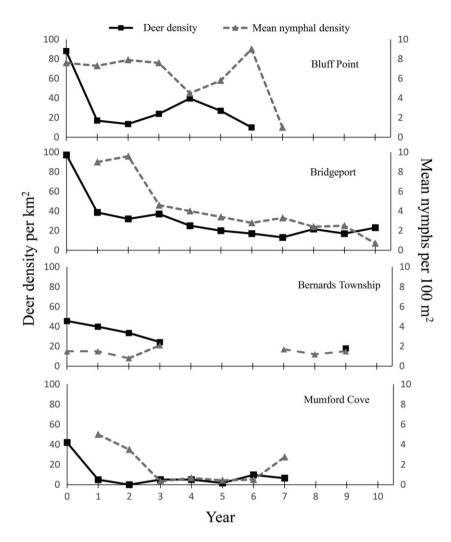
Study location	Size	Ecologic setting	Tick measurement method	Deer density at study start (per km²)	$\label{eq:constraint} \begin{array}{llllllllllllllllllllllllllllllllllll$	Approximate reduction in deer density (%)	Approximate reduction in nymphal <i>I.</i> scapularis (%)	Reduction in human Lyme disease
Monhegan Island, $ME^{\dagger}$ 2.4 km <sup>2</sup> Island	2.4 km <sup>2</sup>	Island	Trapped rats & flagging	44-46	0	100	100	Possible
Great Island, MA*	2.4 km <sup>2</sup>	Island/peninsula	Trapped mice	13-15	<2.3	85	63 (-90%)	Possible
Crane Res., MA	5.7 km <sup>2</sup>	Coastal/island	Trapped mice	61	11	82	50	n/a
Bridgeport, CT	1.8 km²	Fenced	Dragging	97	25	74	90	n/a
		(2.5 m high)						
Bluff Point, CT	3.3 km²	Peninsular	Dragging	92	10	91	06	n/a
Mumford Cove, CT*	1.9 km²	Peninsular	Dragging	21–46	<10	>45	~50	Possible
Bernards Twp, NJ <sup>†</sup>	63.5 km <sup>2</sup>	Inland, open	Dragging	46	18	61	0	No



**Fig. 1.** Deer density and corresponding nymphal *lxodes scapularis* abundance in studies where tick abundance measured as mean number collected per mouse or rat. Year 0 = measurement at the start of deer intervention; data extrapolated from manuscripts when not provided explicitly, and may not be exact.

degree. Blacklegged tick measurements were discontinued in the same year that deer density neared 11 deer per km<sup>2</sup>; therefore, the longer-term effect of the intervention is unknown.

The effect of deer reduction on blacklegged tick abundance was also assessed at two sites in Connecticut, a fenced area of Bridgeport and peninsular Bluff Point (Table 1) (Stafford et al., 2003). At Bridgeport, deer density estimates were based on a marked population. At Bluff Point, estimates were based on aerial surveys, direct observation surveys and the number of deer removed. Beginning in 1992, substantial initial effort rapidly reduced these populations from >90 deer per km<sup>2</sup> at both sites to roughly 39 deer per km<sup>2</sup> at Bridgeport and 17 deer per km<sup>2</sup> at Bluff Point. Subsequent population reduction, gradual at Bridgeport and erratic at the Bluff Point site, eventually reached 10-13 deer per km<sup>2</sup> at both sites (Fig. 2). Immature tick abundance was measured biweekly from May through August by dragging established plots (maximum plots: n = 12 at Bridgeport; n = 9 at Bluff Point) during periods of expected peak



**Fig. 2.** Deer density and corresponding nymphal *Ixodes scapularis* abundance in studies where tick abundance measured as number questing per 100 m<sup>2</sup>. Year 0 is the measurement at the start of the deer intervention; data extrapolated from manuscripts when not provided explicitly and may not be exact.

activity for each stage. Immature *I. scapularis* abundance fluctuated at both sites over the study period. While there was significant correlation between deer density and declining nymphal abundance at Bridgeport ( $r_s = 0.867$ , P < 0.0001), no correlation was noted at Bluff Point ( $r_s = 0.394$ , P = 0.243).

In a separate study in peninsular Mumford Cove, Connecticut, the deer population was rapidly reduced from between 21 and 46 deer per km<sup>2</sup> (estimates of initial density differ between two publications) to approximately five deer per km<sup>2</sup> after special shotgun-archery hunts in 2000 and 2001 (Table 1) (Kilpatrick and LaBonte, 2003; Kilpatrick et al., 2014). Deer density was estimated by roadside direct observation surveys, aerial surveys, radio collaring and application of a correction factor for unobserved deer. Deer density was maintained at <10 deer per km<sup>2</sup> for the following 7 years through maintenance archery harvest (Kilpatrick et al., 2014). Nymphal abundance was assessed by dragging residential lawns and forested sites beginning the spring following the deer reduction; however, insufficient data are presented to evaluate the robustness of the sampling effort. Additionally, nymphal abundance was measured in only one season before an effect of deer reduction would be expected, and no other control plots were sampled, preventing a robust statistical analyses of the effect of the intervention on questing nymphs. Nevertheless, average nymphal abundance on both residential lawns and forested plots appeared to decrease following the intervention, although abundance was notably higher in the final year of measurement despite minimal change in corresponding deer densities.

In concert with an existing deer management programme occurring in inland Bernards Township, New Jersey, tick abundance was monitored by dragging at 10 sites within close proximity to baited deer hunting areas ('cull sites') and 10 sites in neighbouring communities without active deer reduction ('control sites') (Table 1) (Jordan et al., 2007). Initial deer density of 46 deer per km<sup>2</sup> in 2002 (determined by aerial survey) declined to  $\approx 24$  deer per km<sup>2</sup> in 2005 (based on harvest and demographic parameter estimates). Larval and nymphal abundance were notably lower at cull sites than control sites from the beginning and no significant effect of the community deer management effort on tick abundance was detected (Fig. 2). Subsequently, ongoing deer management further reduced deer density (as estimated by aerial survey in 2011) to 18 deer per km<sup>2</sup> (CDC and Bernards Township Deer Management Advisory Committee, unpublished data). Dragging surveys at the same cull and control sites during 2009–2011 continued to show no association between deer density reduction and questing tick abundance (CDC, R. Jordan and T. Schulze, unpublished data).

#### Effect of deer control on Lyme disease incidence

The potential value of deer control as a Lyme disease prevention method depends not solely on decline in blacklegged tick abundance but on whether that decline ultimately translates to a mitigation of human disease risk. Unfortunately, few studies have considered the effect of deer population reduction on human-based outcomes. The Crane Reservation, Bridgeport and Bluff Point interventions were conducted in relatively unpopulated areas. Lyme disease incidence was assessed among the 162 residents of Great Island during 1979-1983. Initially, Lyme disease affected four residents per year, although that rate halved by the time deer reduction began in late 1982 (Steere et al., 1986). Following deer removal, Lyme disease reportedly occurred infrequently among Great Island residents, affecting two persons in the following decade (Telford, 1993, 2002), although the nature of a case definition and method of ascertainment were not provided. Furthermore, any observed decrease in incident cases could also have been the result of other factors (e.g. improved diagnostic methods or increased vigilance in use of personal protective measures) that were not assessed. Likewise, human disease data were not included in the original Monhegan Island study. However, prior to deer removal in the 1990s, 10 of the ~75 permanent Monhegan Island residents had contracted Lyme disease, while two cases among island residents were reported to the public health system during 2001–2011 following deer elimination (Rand et al., 2000, 2004) (Peter Rand, Maine Medical Center, personal communication, and Maine CDC, unpublished data).

In Mumford Cove, a community survey was conducted to assess attitudes about deer population management and the frequency of self-reported physician-diagnosed Lyme disease among residents. Residents reported 17 cases of Lyme disease in the year of the intervention and five cases in the first year following initial deer removal (Kilpatrick and LaBonte, 2003). There are two major limitations to this finding: first, the method of case ascertainment lacks standardization and is subject to bias associated with awareness

of the intervention (i.e. placebo effect); and second, because of the role of deer in the 2-year lifecycle of the blacklegged tick (primarily feeding adult ticks), deer reduction should not impact nymphal tick populations, the principal source of human infections, until the second transmission season following the intervention. Therefore, the reported decrease in human cases observed in the year following deer removal lacks biological plausibility. Additional surveys of the ~100 households in Mumford Cove revealed a consistently lower number of self-reported cases of Lyme disease in the years following the initial deer reduction (Kilpatrick et al., 2014). Unfortunately, the use of linear regression to analyse nonlinear data limits interpretability of the statistical significance of the reported correlations. In a separate effort, Garnett and others evaluated the impact of the Mumford Cove deer reduction on Lyme disease cases reported to the public health system, a method of case ascertainment not subject to the same limitations as self-report (Garnett et al., 2011). Specifically, they compared mean incidence of erythema migrans rash (EM) per 100 000 residents before and after the intervention (accounting for the expected minimum 2-year lag of impact of deer reduction on human disease) in both Mumford Cove and neighbouring 'control' communities. Mean EM incidence did not differ significantly before and after the intervention in Mumford Cove, nor in the control areas.

In Bernards Township, the deer management programme had no demonstrable effect on human Lyme disease incidence (as measured by confirmed cases reported to the New Jersey Department of Health and Senior Services [NJDHSS]) (Jordan et al., 2007). Subsequent examination of human surveillance data revealed an overall decrease in Lyme disease incidence in Bernards Township since the inception of the deer management programme; however, that trend was mirrored by a similar decrease in human incidence in surrounding communities lacking organized deer management (CDC, NJDHSS, unpublished data).

## Evaluation of the evidence

The evidence summarized above suggests that elimination of deer from ecologically isolated settings can have a substantial effect on the reproduction of blacklegged ticks. The results of deer population reduction short of elimination have been mixed, however, and evidence of an effect on human disease risk is limited. The studies conducted at Great Island, Crane Reservation, Bridgeport and Mumford Cove indicate some decrease in nymphal tick abundance following reduction in the local deer population (depending on the statistical analysis conducted), while results of the intervention at Bluff Point were even more equivocal, and there was no appreciable decline in nymphal abundance in Bernards Township. Fundamental differences across studies in ecologic setting, measurement methods, unmeasured abundance of alternate hosts for adult ticks, and starting and ending deer and tick densities complicate quantitative meta-analysis and understanding of this body of evidence as a whole. Moreover, if success of interventions is measured solely by statistically significant reductions in abundance of questing ticks, this outcome is dependent not only on the robustness of sampling, but is also statistically easier to demonstrate in circumstances with higher initial sampled tick densities.

# Generalizability

With the exception of the Bernards Township study, all studies reviewed here were conducted in settings that restricted deer immigration. These settings are not representative of the majority of communities at high risk for Lyme disease. As the abundance and distribution of other tick hosts were not well described or quantified in these studies, it is not possible to assess effects of alternate host availability on tick abundance or reproduction that may have confounded the observed results.

Removal of a large proportion of the deer in any given area may have unanticipated effects on the broader Lyme disease enzootic cycle in both the short and longer term. For example, while deer are a preferred host for adult ticks, in circumstances where deer are plentiful, a portion of larval or nymphal ticks feeding on uninfected deer rather than on infected reservoir hosts could serve to limit or 'dilute' the local infection prevalence in ticks (Lacombe et al., 1993; Perkins et al., 2006). Broad population reduction could, at least temporarily, increase human risk of disease by increasing the number of questing adults seeking alternate hosts and by increasing infection prevalence among nymphs (Deblinger et al., 1993; Mount et al., 1997; Ginsberg and Zhioua, 1999; Rand et al., 2004). Incomplete understanding of these effects limits the ability to generalize findings from published studies that seek to link specific deer densities, tick abundance and Lyme disease risk.

The concept of a threshold deer density below which the enzootic cycle of Lyme disease is interrupted and transmission halts was first suggested by Wilson and colleagues following the Great Island elimination, as they noted that halving the deer density (to approximately seven deer per  $\rm km^2$ ) had no effect on tick abundance whereas essentially eliminating deer resulted in a marked decreased in both larval and nymphal abundance. Efforts to identify a generalizable threshold below which tick abundance and human risk will be reduced have been met with limited scientific support. Elimination of deer from some limited situations where alternate hosts for adult ticks are absent may result in the collapse of tick populations. There is also some evidence that significant reduction in local deer abundance

short of elimination may have measurable, but variable, effects on tick abundance. However, data published to date is far from clear or consistent. This evidence provides fertile ground for hypothesis generation and testing, but does not yet warrant conclusions that can be broadly applied.

# Validity of measured endpoints

In the studies reviewed here, some measure of nymphal tick abundance has been used as the surrogate for human Lyme disease risk. Nevertheless, a direct relationship between nymphal tick density and human disease risk has not been consistently demonstrated because of varying robustness of sampling effort and assessment of tick abundance and human disease risk at widely different spatial scales (Nicholson and Mather, 1996; Kitron and Kazmierczak, 1997; Connally et al., 2006; Diuk-Wasser et al., 2012; Pepin et al., 2012). Because of limited human population in areas where most of these studies were performed, suitably powered assessment of the effect of deer interventions on human illness has not been possible. Although self-reported Lyme disease declined in Mumford Cove following deer removal, assessment of disease incidence as reported to the public health system revealed no difference when compared to incidence in neighbouring areas. While surveillance data are subject to limitations of underreporting, public health surveillance is infinitely more reliable than anecdote and self-report, which are subject to changes in individual behaviour, recall bias and lack of a standardized case definition. Reproducible demonstration of reduced Lyme disease cases, assessed in a standardized manner and coupled with a clear decline in nymphal blacklegged tick abundance, would be necessary to demonstrate the efficacy of deer population control as a public health intervention for Lyme disease.

# Feasibility

Deer management is a politically charged issue in many communities in the United States (Decker and Chase, 1997; Rutberg, 1997; Stout et al., 1997; Loker et al., 1999; Conover, 2002; Williams et al., 2013). Wildlife managers face the challenging task of maintaining the local deer herds at levels that are biologically sound, while balancing hunters' desires and residents' feelings regarding the aesthetic value of deer and the acceptability of different management methods. Public support for deer management depends on several factors, including personal experience, perceptions regarding negative effects of overpopulation, as well as the cost to taxpayers for programmes that can last years before benefits are realized (Stout et al., 1997; Kilpatrick et al., 2007).

In most settings, a large proportion of the deer population must be removed each year to lower overall density. Lethal control methods that reduce deer populations below the local biological carrying capacity may be counteracted by increased immigration and higher reproductive capacity in areas with reduced density (Conover, 2002; Keyser et al., 2005). As a result, population reduction over a wide area is likely to be more effective than in a small area, such as a single community, that is ecologically open to surrounding areas (Conover, 2002). Consequently, in an island setting not subject to deer immigration, complete elimination of the herd, or maintenance of a deer population at a low density, may be both more biologically feasible and politically sustainable, whereas inland settings may have more difficulty achieving the desired low deer density and maintaining the political will to sustain a resource-intensive effort over many years.

# Conclusions

Deer overpopulation can have dramatic negative effects on the landscape. Intervention to limit deer overpopulation can improve herd health, mitigate forest and crop damage, improve overall ecosystem health and reduce motor vehicle collisions. However, as summarized here, the scientific evidence to support the effectiveness of deer control as a means of preventing human Lyme disease is weak. While complete elimination of deer in an ecologically isolated setting with few alternative hosts for adult ticks may substantially reduce the blacklegged tick population, results have been mixed in circumstances where deer are not eliminated. Furthermore, evidence linking deer reduction to reduced human Lyme disease risk is lacking. Robust, reproducible scientific evidence should support any recommended public health intervention, let alone one that is both costly and controversial.

Entomologic measures do not always correlate with human risk, which underscores the need to evaluate the efficacy of interventions by assessing not only tick abundance but also systematically assessed human-tick encounters or human disease. As the public health burden of Lyme disease in the United States continues to expand, there is clear need for novel prevention methods or broader implementation of existing methods. Research is needed that translates successful tick control interventions to quantifiable public health impact. Although community-wide prevention measures are appealing, beyond deer reduction, to our knowledge the only other described measure which acts at a community level is topical acaricide treatment of deer (via four poster devices) (Hayes and Piesman, 2003; Fish and Childs, 2009). Although acaricide treatment of deer may be more feasible than substantial deer population reduction in inland settings, evaluation of the effectiveness of this method in preventing human illness is needed and widespread implementation is met with substantial logistic hurdles; these details of are beyond the scope of this review.

Demonstrating reduced human disease risk after implementation of community-level interventions can be challenging, as it requires expensive, long-term assessment replicated in a large number of communities - financial support for such comprehensive research is limited. Future research efforts to address deer reduction as a potential means of reducing Lyme disease risk should include multidisciplinary input from entomologists, wildlife biologists and epidemiologists, and could assess: (i) the impact of deer elimination on larger islands with a substantial human population and high rates of Lyme disease; (ii) the feasibility and effect of sustaining low-density deer populations in inland communities; (iii) the potential for additive effects of deer reduction in concert with other tick control methods; and (iv) the effect of these efforts on systematically measured human-tick encounters or tickborne illness. The benefit in reducing human disease will need to be clearly demonstrated for communities to be able to effectively weigh against costs for adoption of any tick control method, alone or as part of a local integrated tick control programme.

# Acknowledgements

The authors would like to thank Shereen Semple of the New Jersey Department of Health and Senior Services. Funding was provided by CDC.

# **Conflict of Interest**

No conflict of interests declared.

# References

- Anderson, J. F., and L. A. Magnarelli, 1980: Vertebrate host relationships and distribution of ixodid ticks (Acari: Ixodidae) in Connecticut, USA. J. Med. Entomol. 17, 314–323.
- Connally, N. P., H. S. Ginsberg, and T. N. Mather, 2006: Assessing peridomestic entomological factors as predictors for Lyme disease. J. Vector. Ecol. 31, 364–370.
- Conover, M., 2002: Resolving Human-Wildlife Conflicts: the Science of Wildlife Damage Management. Lewis Publishers, Boca Raton.
- Daniels, T. J., and D. Fish, 1995: Effect of deer exclusion on the abundance of immature *Ixodes scapularis* (Acari: Ixodidae) parasitizing small and medium-sized mammals. *J. Med. Entomol.* 32, 5–11.
- Daniels, T. J., D. Fish, and I. Schwartz, 1993: Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease risk by deer exclusion. *J. Med. Entomol.* 30, 1043–1049.

Deblinger, R. D., M. L. Wilson, D. W. Rimmer, and A. Spielman, 1993: Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following incremental removal of deer. *J. Med. Entomol.* 30, 144–150.

Decker, D. J., and L. C. Chase, 1997: Human dimensions of living with wildlife: a management challenge for the 21st century. *Wildl. Soc. Bull.* 25, 788–795.

Diuk-Wasser, M. A., A. G. Hoen, P. Cislo, R. Brinkerhoff, S. A.
Hamer, M. Rowland, R. Cortinas, G. Vourc'h, F. Melton, G. J.
Hickling, J. I. Tsao, J. Bunikis, A. G. Barbour, U. Kitron, J.
Piesman, and D. Fish, 2012: Human risk of infection with Borrelia burgdorferi, the Lyme disease agent, in eastern United States. Am. J. Trop. Med. Hyg., 86, 320–327.

Duffy, D. C., S. R. Campbell, D. Clark, C. DiMotta, and S. Gurney, 1994: *Ixodes scapularis* (Acari: Ixodidae) deer tick mesoscale populations in natural areas: effects of deer, area, and location. *J. Med. Entomol.* 31, 152–158.

Elias, S. P., R. P. Jr Smith, S. R. Morris, P. W. Rand, C. Lubelczyk, and E. H. Lacombe, 2011: Density of *Ixodes scapularis* ticks on Monhegan Island after complete deer removal: a question of avian importation? *J. Vector. Ecol.* 36, 11–23.

Fish, D., and J. E. Childs, 2009: Community-based prevention of Lyme disease and other tick-borne diseases through topical application of acaricide to white-tailed deer: background and rationale. *Vector Borne Zoonotic. Dis.* 9, 357–364.

Garnett, J. M., N. P. Connally, K. C. 3rd Stafford, and M. L. Cartter, 2011: Evaluation of deer-targeted interventions on Lyme disease incidence in Connecticut. *Public Health Rep.* 126, 446–454.

Ginsberg, H. S., and E. Zhioua, 1999: Influence of deer abundance on the abundance of questing adult *Ixodes scapularis* (Acari: Ixodidae). *J. Med. Entomol.* 36, 376–381.

Ginsberg, H. S., E. Zhioua, S. Mitra, J. Fischer, P. A. Buckley, F. Verret, H. B. Underwood, and F. G. Buckley, 2004: Woodland type and spatial distribution of nymphal *Ixodes scapularis* (Acari: Ixodidae). *Environ. Entomol.* 33, 1266–1273.

Hayes, E. B., and J. Piesman, 2003: How can we prevent Lyme disease? *N. Engl. J. Med.* 348, 2424–2430.

Jordan, R. A., and T. L. Schulze, 2005: Deer browsing and the distribution of *Ixodes scapularis* (Acari: Ixodidae) in Central New Jersey forests. *Environ. Entomol.* 34, 801–806.

Jordan, R. A., T. L. Schulze, and M. B. Jahn, 2007: Effects of reduced deer density on the abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease incidence in a northern New Jersey endemic area. *J. Med. Entomol.* 44, 752–757.

Keyser, P. D., D. C. Jr Guynn, and H. S. Jr Hill, 2005: Densitydependent recruitment patterns in white-tailed deer. *Wildl. Soc. Bull.* 33, 222–232.

Kilpatrick, H. J., and A. M. LaBonte, 2003: Deer hunting in a residential community: the community's perspective. *Wildl. Soc. Bull.*, 31, 340–348.

Kilpatrick, A. M., and S. E. Randolph, 2012: Drivers, dynamics, and control of emerging vector-borne zoonotic diseases. *Lancet* 380, 1946–1955. Kilpatrick, H. J., A. M. LaBonte, and J. S. Barclay, 2007: Acceptance of deer management strategies by suburban homeowners and bowhunters. *J. Wildl. Manage*. 71, 2095–2101.

Kilpatrick, H. J., A. M. LaBonte, and K. C. Stafford, 2014: The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. *J. Med. Entomol.* 51, 777–784.

Kitron, U., and J. Kazmierczak, 1997: Spatial analysis of the distribution of Lyme disease in Wisconsin. *Am. J. Epidemiol.* 145, 558–565.

Lacombe, E., P. W. Rand, and R. P. Jr Smith, 1993: Disparity of *Borrelia burgdorferi* infection rates of adult *Ixodes dammini* on deer and vegetation. *J. Infect. Dis.* 167, 1236–1238.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers, 2012: Deer, predators, and the emergence of Lyme disease. *Proc. Natl. Acad. Sci. U S A* 109, 10942–10947.

Loker, C. A., D. J. Decker, and S. J. Schwager, 1999: Social acceptability of wildlife management actions in suburban areas: 3 Cases from New York. *Wildl. Soc. Bull.* 27, 152–159.

Main, A. J., H. E. Sprance, K. O. Kloter, and S. E. Brown, 1981: *Ixodes dammini* (Acari: Ixodidae) on white-tailed deer (*Odo-coileus virginianus*) in Connecticut. J. Med. Entomol. 18, 487–492.

Mather, T. N., S. R. 3rd Telford, S. I. Moore, and A. Spielman, 1990: *Borrelia burgdorferi* and *Babesia microti*: efficiency of transmission from reservoirs to vector ticks (*Ixodes dammini*). *Exp. Parasitol.* 70, 55–61.

Mead, P. S., 2011: Education, Behavior Change, and Other Non-Pharmaceutical Measures Against Lyme and Other Tick-Borne Diseases. Critical Needs and Gaps in Understanding Prevention, Amelioration, and Resolution of Lyme and Other Tick-Borne Diseases: The Short-Term and Long-Term Outcomes: Workshop Resport. Institute of Medicine, Washington DC.

Mount, G. A., D. G. Haile, and E. Daniels, 1997: Simulation of blacklegged tick (Acari: Ixodidae) population dynamics and transmission of *Borrelia burgdorferi. J. Med. Entomol.* 34, 461–484.

Nicholson, M. C., and T. N. Mather, 1996: Methods for evaluating Lyme disease risks using geographic information systems and geospatial analysis. *J. Med. Entomol.* 33, 711–720.

Ostfeld, R. S., 2011: Lyme disease: the ecology of a complex system. Oxford University Press, New York.

Pepin, K. M., R. J. Eisen, P. S. Mead, J. Piesman, D. Fish, A. G. Hoen, A. G. Barbour, S. Hamer, and M. A. Diuk-Wasser, 2012: Geographic variation in the relationship between human Lyme disease incidence and density of infected hostseeking *Ixodes scapularis* nymphs in the Eastern United States. *Am. J. Trop. Med. Hyg.* 86, 1062–1071.

Perkins, S. E., I. M. Cattadori, V. Tagliapietra, A. P. Rizzoli, and P. J. Hudson, 2006: Localized deer absence leads to tick amplification. *Ecology* 87, 1981–1986.

Piesman, J., and A. Spielman, 1979: Host-associations and seasonal abundance of immature *Ixodes dammini* in southeastern Massachusetts. Ann. Entomol. Soc. Am. 72, 829–832. Piesman, J., A. Spielman, P. Etkind, T. K. 2nd Ruebush, and D. D. Juranek, 1979: Role of deer in the epizootiology of *Babesia microti* in Massachusetts, USA. *J. Med. Entomol.* 15, 537–540.

Piesman, J., J. G. Donahue, T. N. Mather, and A. Spielman, 1986: Transovarially acquired Lyme disease spirochetes (*Borrelia burgdorferi*) in field-collected larval *Ixodes dammini* (Acari: Ixodidae). J. Med. Entomol. 23, 219.

Rand, P. W., E. H. Lacombe, M. S. Holman, C. Lubelczyk, and R. P. Jr Smith, 2000: Attempt to control ticks (Acari: Ixodidae) on deer on an isolated island using ivermectin-treated corn. J. Med. Entomol. 37, 126–133.

Rand, P. W., C. Lubelczyk, G. R. Lavigne, S. Elias, M. S. Holman, E. H. Lacombe, and R. P. Jr Smith, 2003: Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). *J. Med. Entomol.* 40, 179–184.

Rand, P. W., C. Lubelczyk, M. S. Holman, E. H. Lacombe, and R. P. Jr Smith, 2004: Abundance of *Ixodes scapularis* (Acari: Ixodidae) after the complete removal of deer from an isolated offshore island, endemic for Lyme disease. *J. Med. Entomol.* 41, 779–784.

Rutberg, A. T., 1997: Lessons from the urban deer battlefront: a plea for tolerance. *Wildl. Soc. Bull.* 25, 520–523.

Schulze, T. L., M. F. Lakat, G. S. Bowen, W. E. Parkin, and J. K. Shisler, 1984: *Ixodes dammini* (Acari: Ixodidae) and other ixodid ticks collected from white-tailed deer in New Jersey, USA.
I. Geographical distribution and its relation to selected environmental and physical factors. *J. Med. Entomol.* 21, 741–749.

Schulze, T. L., R. A. Jordan, and R. W. Hung, 2001: Potential effects of animal activity on the spatial distribution of *Ixodes scapularis* and *Amblyomma americanum* (Acari: Ixodidae). *Environ. Entomol.* 30, 568–577.

Stafford, K. C. 3rd, 1993: Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) with exclusion of deer by electric fencing. *J. Med. Entomol.* 30, 986–996.

Stafford, K. C. 3rd, 2007: Tick Management Handbook: An integrated guide for homeowners, pest control operators, and public health officials for the prevention of tick-associated disease. The Connecticut Agricultural Experiment Station, New Haven.

Stafford, K. C. 3rd, A. J. Denicola, and H. J. Kilpatrick, 2003: Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and the tick parasitoid *Ixodiphagus hookeri* (Hymenoptera: Encyrtidae) with reduction of white-tailed deer. *J. Med. Entomol.* 40, 642–652.

Steere, A. C., E. Taylor, M. L. Wilson, J. F. Levine, and A. Spielman, 1986: Longitudinal assessment of the clinical and epidemiological features of lyme disease in a defined population. J. Infect. Dis. 154, 295–300.

- Stout, R. J., B. A. Knuth, and P. D. Curtis, 1997: Preferences of suburban landowners for deer management techniques: a step toward better communication. *Wildl. Soc. Bull.* 25, 348–359.
- Telford, S. R. 3rd, 1993: The forum: perspectives on the environmental management of ticks and Lyme disease. In: Ginsberg, H. S. (ed), Ecology and Environmental Management of Lyme disease. Rutgers University Press, New Brunswick, NJ.
- Telford, S. R. 3rd, 2002: Deer tick-transmitted zoonoses in the Eastern United States. In: Aguirre, A., R. S. Ostfeld, G. M. Tabor, C. House, and M. C. Pearl (eds), Conservation medicine: ecological health in practice. Oxford University Press, New York.
- Telford, S. R. 3rd, T. N. Mather, S. I. Moore, M. L. Wilson, and A. Spielman, 1988: Incompetence of deer as reservoirs of the Lyme disease spirochete. Am. J. Trop. Med. Hyg. 39, 105–109.
- Werden, L., I. K. Barker, J. Bowman, E. K. Gonzales, P. A. Leighton, L. R. Lindsay, and C. M. Jardine, 2014: Geography, deer, and host biodiversity shape the pattern of Lyme disease emergence in the Thousand Islands Archipelago of Ontario, Canada. *PLoS One* 9, e85640.
- Williams, S. C., A. J. Denicola, T. Almendinger, and J. Maddock, 2013: Evaluation of organized hunting as a management technique for overabundant white-tailed deer in suburban landscapes. *Wildl. Soc. Bull.* 37, 137–145.
- Wilson, M. L., J. F. Levine, and A. Spielman, 1984: Effect of deer reduction on abundance of the deer tick (*Ixodes dammini*). *Yale. J. Biol. Med.* 57, 697–705.
- Wilson, M. L., G. H. Adler, and A. Spielman, 1985: Correlation between abundance of deer and that of the deer tick, *Ixodes dammini* (Acari: Ixodidae). *Ann. Entomol. Soc. Am.* 78, 172– 176.
- Wilson, M. L., S. R. 3rd Telford, J. Piesman, and A. Spielman, 1988: Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following elimination of deer. *J. Med. Entomol.* 25, 224–228.
- Wilson, M. L., T. S. Litwin, T. A. Gavin, M. C. Capkanis, D. C. Maclean, and A. Spielman, 1990a: Host-dependent differences in feeding and reproduction of *Ixodes dammini* (Acari: Ixodidae). *J. Med. Entomol.* 27, 945–954.
- Wilson, M. L., A. M. Ducey, T. S. Litwin, T. A. Gavin, and A. Spielman, 1990b: Microgeographic distribution of immature *Ixodes dammini* ticks correlated with that of deer. *Med. Vet. Entomol.* 4, 151–159.